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I.—*Considerations respecting Spur-shaped Nectaries, and those of the* Aquilegia vulgaris *in particular.* By M. Ch. Morren, Professor in ordinary at the University of Liége, Member of the Royal Academy of Brussels, &c.*

[With a Plate.]

THE Columbine, that pretty ranunculaceous flower of our woods, deserves attention, as well on account of its structure, curious as it is, and, we venture to add, but little known, as from the historical recollections which it brings to mind. To say nothing here of the medicinal virtues which Dioscorides attributed to his *Isopyron* or to his *Phasiolon*,—a plant which Fabius Columna, Clusius, Dodonæus and many other learned botanists suppose to be no other than the Columbine itself; and not to mention Adrian Junius, who also quotes it as a medical plant; or Francois Rapard, a celebrated physician of Bruges, who addressed to Clusius a letter upon its uses in difficult labours; ought we not to remark that its singular nectaries, compared by some to the beak and talons of an eagle, by others to the graceful neck of the pigeon, by some to rams'-horns, and by others to capuchins' hoods, had so gained the attention of the painters of the middle ages, that it became one of the favourite flowers, placed in great profusion in the illuminations of missals and manuscripts of the time? The '*ancoiles*' or the '*ancolyes*' were there intermixed with the leaves, flowers, or fruit of the strawberry or of the campanula; and Memling was most particularly attached to it. When Dodoens wrote his "Trÿdt-Boeck," the name *Aquileia* or *Aquilina* was still a novelty *just introduced*, he says, by the latest phytographers of his own time. The name *Aquilegia*

* Translated from the original communicated by the Author.

which he gives it calls to mind the comparison already mentioned, of the beak and talons of an eagle; but since that time that of *Columbine* prevailed in England and in Holland, where they were fonder of likening the spurred petal of this flower to the stately neck of a pigeon. When one of these flowers is turned upside-down, says an English author *, we might fancy we saw a group of young eagles, or, if we like better, a nest of pigeons. It is evident that these spur-shaped nectaries had considerable influence on the mind of Dodoens, since on their account he places his *Akeleyen* (*'ancolies,'* columbines,) between the *Cypripedium Calceolus*, a monocotyledonous plant, and his *Orant* or *Antirrhinum majus*,—an alliance which would not at all square with our present ideas of classification by families. By a singular chance, the *Cypripedium*, which in our mythological language we call the *Venus's foot*, was at that period of religious struggles called *Our Lady's shoe* (*Calceolus Mariæ*), and the *Columbine* was named in its turn *the Virgin's glove*: thus we see that shoes and gloves shook hands in our Lady's toilet.

Chief ornament of the gardens of the middle ages, and even of those of the sixteenth century, the *Aquilegia*, carefully and almost universally cultivated, produced those varieties which modern botanists have pointed out in this species. Joost van Ravelingen, the commentator of Dodoens, and L'Obel †, mention the varieties in colour and those of form to be met with in their time: blue, red, flesh-coloured, blue and white, white and variegated. The garden of a gentleman of Leyden, Jean van Hogelande, produced an *Aquilegia pleno flore roseo*, which Clusius described and illustrated. The same botanist had also recorded a variety truly monstrous (*Aquilegia degener*), in that the petals, being reduced to their primitive type of leaves, had remained green; only Van Ravelingen did not think that such monstrosities were worth the pains of describing. Now-a-days we should be eager to do it, and not without reason; for the organography of such a flower is very interesting to know, in relation to the subject which will occupy us further on.

The varieties of structure known under the name of *Aquilegia vulgaris corniculata*, in which Biria ‡ and DeCandolle § discovered that the cornets are deviations of the anther,

* Burnett's Outlines of Botany, p. 840.

† Generally written Lobel; but the true name of the author of the *Stirpium Historia* was Matthias De L'Obel, as appears from his letters and the portrait engraved during his life-time.

‡ Biria. Monographie des Rénonculacées. Montpellier, 1811.

§ DeCandolle. Organographie, tom. i. p. 496.

and those which bear the name of *Aquilegia vulgaris ecalcarata* or *stellata*, in which, according to these authors, the petals proceed from modified staminal filaments without anthers—these varieties had been already described by Clusius, Dodoens and L'Obel*. Moreover, these authors, besides the simple, semi-double and double varieties of these two principal forms (true sub-varieties which we still possess), also mention Columbines with inverted flowers (*Aquileia flore inverso variegato*). We might suppose, from the Dodonæan context, that it was hereby understood that the flowers, instead of being pendent, were upright ..... "die niet en verschillen van de ander dan dat de bloemen averechts staen." But we know that in this variety, the bases of the spurs being twisted, the spur itself has an upward direction.

We cannot but take an interest in observing the pleasures of the horticulturists of those times. Now-a-days these Columbines are treated with disregard, and dismissed as fit only for the garden of the cottager or village Curé, or, at most, are only permitted to grow in the shade of some forgotten nook of our villas; but let us not say too much: fashion, which revives all antiquated things, may some day assert its claim upon these Columbines of the Castels. Already in the Botanic Garden at Brussels, we have seen pretty borders entirely filled with this plant of the middle ages.

The Columbine is really a very interesting flower, on account of its nectaries; and their genesis not being known, at least so far as we are aware, we have taken them as the principal subject of our researches: our object has been to study them comparatively in the different varieties of the common species, and in some other species which we had at hand; secondly, to observe the monstrous structures; thirdly, to take them at their different degrees of evolution, in order to establish their true genesis; and, lastly, to examine their histology, so as to ascertain how in their forms so varied the interior tissues were affected.

So long as the laws of metamorphoses had not acquired the right of citizenship in the domains of science, calcariform nectaries had to be considered as special pieces, born *ad hoc*, and being such by their proper nature, without an anterior nature, without a type from which they were derived. Although Linnæus had said, "*Si nectarium a petalis distinctum, communiter ludit*;" he also said, "*distincta esse nectaria a corolla constat exemplis: Aconitum, Aquilegia*," &c.†.—They were, then, the floral pieces whose secretion of honey determined

* Dodoens. Cruydt-Boek, 1644, p. 274.

† Linnæi Philosophia Botanica: Fructificatio i. 110.

their character, and that character raised them to the rank of organs *sui generis*, not proceeding from any other:—they were, because they were.

They were, however, not nectaries, because by their nature they were stamens: here is that truth which science had not then become possessed of.

But when, at the end of the last century, Gœthe, following the example of Wolff, established his celebrated theory of the metamorphosis of plants, the nectaries at once lost their autochthonous nature; they were no longer aboriginal organs. On the contrary, in this new theory the nectaries became essentially organs of transition, mere forms of anterior organs; they were, in short, *intermediary organs of passage between the petals and the stamens**. In the spirit of this philosophic method, it was necessary to understand, that in order for the petal to become a stamen, in an ascending metamorphosis, it must previously pass through the form of a nectary. Moreover, Gœthe, who took precisely the Columbine as the example of one of the most remarkable and most striking transformations, considered, as he says, the cuculliform nectaries of this flower as a derivation from the petals†. We shall see, on the contrary, that the progress of nature is a descending metamorphosis; that is to say, that the nectary is, in its genesis, a stamen, and subsidiarily, that a stamen being developed as such, it may afterwards *turn into a nectary*.

The theory of Gœthe had made too little impression in France to admit of the supposition, that in 1815 Mirbel set out from it when he regarded the nectaries of the Columbine, as well as all organs of the same kind, as anomalous forms of the parts of the perianthium. The spur-shaped cornets of the *Aquilegia* were also, in his eyes, forms of petals; but the anomaly attacking all the petals at once, the flower remained *regular* ‡. It was one of the *successive alterations of types*, and in the Columbine particularly this alteration was created in order to become an organ of secretion. A glandular lamina existed for this purpose at the bottom of the cornet-shaped petals §. The petal was the type.

This lamina we have never found; and in the *Aquilegia glandulosa*, the *Aquilegia atrata*, &c., we have seen that there only exist one, or two, or three cornets without the regularity of the flower being perverted, as is the case in the *Nasturtium*,

* Gœthe. Œuvres d'Histoire Naturelle. Edition de Martius et Turpin. Paris, 1837, p. 226.

† Ibid, p. 228, chap. 56.

‡ Mirbel. Elémens de Physiologie, vol. i. p. 269.

§ Gœthe. Œuvres d'Histoire Naturelle. Edition de Martius.

Tropæolum, or the Lark's-spur. The great German poet's notions had not indeed at first all possible success in this country. Willdenow always asserted that the spur (*calcar*) was more an organ intended to preserve the nectar than to prepare it, and that it was furthermore a sacciform elongation of the corolline corona*. The first of these facts is evidently erroneous. The second was also admitted by Jacquin.

Sprengel, when opposing Vaillant, who had also himself declared that the nectary was always a production of the corolla, placed the spurs of the Columbine in his class of *Nectarothecæ*, and characterized by the presence of the secreting gland at the bottom of the cornet. Moreover, it never occurred to his mind to investigate the anterior nature of this apparatus in the *Passifloreæ*, in the Aconites, and a multitude of other plants; he sees only peculiar *little machines*, more or less ornamented: *machinulæ peculiares . . . . . eleganter coloratæ*†.

DeCandolle, in 1819, adopts this view of the subject; but the spur, according to him, is of a very different nature,—an elongation, one while of the calyx, one while of the corolla, one while of the perigonium; but the stamens are still excluded from the floral organs which may produce this nectary‡. However, a year before, the celebrated botanist of Geneva had positively declared that, in the *Aquilegiæ corniculatæ*, without regard to species, the supplementary spurs arose from a modification of the anthers which lengthened downwards; moreover, he recognises the origin of the *stellated* varieties from the abortion of the anthers, and from the hypertrophy of the filaments; and lastly, that the scales which are situated between the carpels and the stamens are stamens without anthers, and with dilated and membranous filaments§. Biria had made known the former facts‖. In 1827 these ideas were again brought forward in the *Organographie végétale*¶. They are, undeniably, the most accordant to the real state of things.

Among the most recent authors we may mention Kurr, who places the spurs of the Columbine with his *nectarostigmata*. A very curious remark of this accurate writer is, that the greenish glands which secrete the nectar at the bottom of

* Willdenow. Grundriss der Krauterkunde, cap. 86–88. (Terminologie.)

† Linnæi Phil. Bot. edit. Sprengel (notes). Fructificatio 110.

‡ DeCandolle. Théorie élémentaire, p. 406, § 395.

§ DeCandolle. Systema Regni Vegetabilis, vol. i. p. 333.

‖ Biria. Histoire naturelle et médicale des Rénoncules, 1 fasc. Montpellier, 1811.

¶ DeCandolle. Organographie, vol. i. pp. 484—496.

the spurred cornet, do not begin to afford this sugared liquid until precisely when the first anther blows. The secretion lasts only as long as the stamens are capable of performing their functions, and at the end of three or four days the flower leaves off this ejection of fluid and of pollen, and drops the organs which produced both the one and the other*. This curious remark is quite correct; we have verified it. From this we might be led to suppose that the secretion of the nectar, which is here so intimately connected with the functions of the stamens, becomes necessary to the action of the sexes; but from ten unblown flowers, where there had been neither dehiscence of the anthers, nor secretion of nectar by the spurs, Kurr cut away those organs: the further development took place without any difference, and these flowers bore as many and as large fruits as they ordinarily do; the seeds germinated as usual†. This experiment gives great support to those who consider the nectar as being only a true excretion, comparable to our urine, and which is of no use, at least in the great majority of cases, in the process of fecundation, as was generally supposed. Kurr, however, does not give his opinion as to the proper nature of the spurs.

Lindley, in his new edition of the 'Introduction to Botany,' (1839) no longer gives (to the great regret of the friends of deep scientific research) the interesting and useful part on morphology; but this judicious author, in his edition of 1832‡, had published some very curious details upon the *Aquilegia vulgaris*. "The petals of this plant," says he, "consist of a long, sessile, purple horn or bag, with a spreading margin, while the stamens consist of a slender filament, bearing a small, oblong, 2-celled, yellow anther. In single and regularly-formed flowers, nothing can be more unlike than the petals and stamens; but in double flowers the transition is complete. The petals which first begin to change, provide themselves with slender ungues: the next contract their margin, and acquire a still longer unguis: in the next the purple margin disappears entirely; two yellow lobes like the cells of the anther take its place, and the horn, diminished in size, no longer proceeds from the base, as in the genuine petal, but from the apex of the now filiform unguis: in the last transition the lobes of the anther are more fully formed, and the horn is almost contracted within the dimensions of the connective, retaining, however, its purple colour: the next stage

* Kurr. Untersuchungen über die Bedeutung, &c. Stutgard, 1833.

† Ibid, p. 128.

‡ Lindley. Introduction to Botany (1832), p. 515.—[Ed. 1835, p. 536.]

is the perfect stamen. No further evidence," says our author, "can, I think, be required of the formation of stamens out of petals."

We see that Lindley had here followed the impulse given by Gœthe, and that he looked upon the cuculliform petals (Richard) as proceeding towards the formation of the stamina by an ascending metamorphosis. At present the spur is no longer in his view anything but a modified petal*. A discovery which we cannot dispute with him, since the germ of it appears in his words, is that the horn of the Columbine is really a lengthened connective,—a thing which we shall also establish by direct proofs hereafter.

Although G. W. Bischoff, Professor of Botany at Heidelberg, does not give this morphological genesis of the spur in the *Aquilegia*, still this author helps to lead us to believe that this is really the means which nature employs, in what he has remarked respecting the metamorphosis of the nectar-bearing horns of the *Helleborus fœtidus* into normal stamens†. Link sees nothing in the spur but a continuation of the petal, characterized by the presence, at the end of its cavity, of a cellular gland, but of which the cellules have walls thicker than ordinary,—a thing which we take the liberty of not admitting‡. After M. Vogel of Bonn had sent me his elegant memoir on the development of the parts of the flower in the Leguminosæ§, the study of the formation of calcariform or cuculliform nectaries, according to the glossology of Richard‖, became still more interesting. Indeed, Schleiden and Vogel having proved, by their labours, that it is not merely in idea, as a mental abstraction, that we are to see in the floral organs nothing but the axis of the plant and its leaves, but that this axis and its green leaves are really and substantially found, placed regularly in the very small buds, we thought that the investigation of the genesis of the nectaries in the Columbine could not be without scientific interest. DeCandolle came to consider these horn-shaped nectaries as anthers, by comparison; Lindley came to the same conclusion by the observation of teratological cases; it was become therefore curious to test these views *à priori* and *à posteriori* by organogenic proofs: and this is what we have proposed to ourselves.

* Lindley. Introduction to Botany (1839), p. 169.

† Gottlob Wilhelm Bischoff. Lehrbuch der Botanik, vol. i. p. 404. (1833.)

‡ Link. Elementa Philosophiæ Botanicæ, vol. ii. p. 130.

§ Schleiden und Vogel. Beitrage zur Entwickelungsgeschichte der Blumentheile bei den Leguminosen. (Act. Nat. Curios. vol. xix. p. 1.)

‖ Richard. Nouv. Elémens de Botanique, 1838, p. 333.

Let us see, first, what takes place in a flower of *Aquilegia vulgaris calcarata.*

1. *Metamorphosis of the stamen into a spur-shaped nectary.*

The stamen of the Columbine has a thread-shaped filament slender, flexible and yellow, and a two-celled anther with parallel cells, slightly swelled, opening with a slit and united by a narrow connective, the whole yellow. The connective is even hardly visible (Plate XI. fig. 1).

In many flowers, we find along the spire which leads insensibly from the androœceum to the corolla, stamens which turn into nectaries. To bring this about, the filament enlarges at its base; the connective is, at the opposite pole, the other organ which becomes modified, and it is even the most active of all in this transformation. It enlarges above, by separating the two loculi of the anther, and it grows to a point. This is not slow in becoming bifurcate, so that the connective is soon bilobate. (Figs. 2 and 7.)

To this modification, which up to this period does not attack the regularity of the organ, two ways of transformation succeed. In the one, one of the loculi of the anther disappears, in the other it remains visible with its fellow. The first of these modifications might induce a belief that *the spur is a sac formed by one half of an anther or by a loculus,* but this genesis is but a deceitful appearance. The second way of transformation proves *that the spur is a sac-shaped connective, and that the two lobes of its limb represent the two loculi of the anther originally united by this same connective.*

If such a spur-shaped nectary can be obtained, as from its nectar-secreting gland is truly a nectary, and that in it the two lobes of its limb exist as an elongation of the two anther-cells, still visible enough to attest their presence, it is clear that this second way of transformation should be admitted. Now this is precisely what experience confirms. In the Columbine we find this form, not so frequently as the first, it is true; but it is found, and that is all that is necessary. This case we have delineated (Plate VII. fig. 6). On a stamen thus modified, besides a well-formed filament (*c h*), we find the two loculi of the anther, still bearing pollen, but which open more widely (*a b*), separated by a small connectival eminence (*c*). Each of the swellings which represent the anther-cells produces an elongation in form of a thick margin (*e*), which, reaching from the inside to the outside, goes to form the circumference of the two lobes of the cornet (*d g*), separated by a slit (*f*). Each lobe corresponds to a cell, and originates from it; it is only indeed that same cell length-

ened. Lastly, *i* represents the belly of the cornet, and at *k* we find the gland which, for its part, secretes whilst the pollen no longer issues from the loculi, and little by little its structure is annihilated.

This case of metamorphosis not only proves, as we said above, that the two lobes of the cornet of the Columbine are derivations from the cells of the anther, but it puts out of doubt that the tube of the cornet is the lengthened connective. A circumstance which we must not lose sight of in this philosophic study of a metamorphosed flower, is that the nectar-bearing gland, an organ of emission, and which rids the flower of its excess of carbon, is found at the opposite pole to the pollen-bearing loculi, other organs of emission which also excrete from the individual, but in this case for the preservation of the species, a substance eminently charged with carbon. At the two poles then the same function exists, but the one does not begin till the other ceases; that is to say, the nectarial gland does not exist or become developed until the pollen apparatus wastes away and becomes obsolete. This subject certainly merits a reflection; even should I be accused of seeing, in Botany, more than my own eyes *can* see, and especially should I be accused of allowing to myself, in a science of observation, some stretch of imagination. For my part, I could never comprehend how inquiry into the truths of nature should put aside the understanding, and reduce it to a state of inaction which would render it useless. Behind and above facts I always conceive something superior and anterior; for facts are *effects*, and it is to the knowledge of *causes* that we ought to endeavour to come. Now here, in the particular problem which occupies us, I see a verification of the law of *organic compensation* and a realization of the *unity of composition*. Thus, the *nectaries* are ONE with the *stamens*, the *stamens* ONE with the *leaves*, the leaves ONE with themselves, as autochthonous organs. So much for the law of *unity*. Moreover, the *gland* is at the *end* of the nectary, because, by its nature a stamen, the *pollen* is at the other *end*; there is a change in the product, but not a change of nature, and by the side of this law of *polarity* there is that of *compensation*; for, in proportion as the anther-cell closes to render the pollen *abortive*, there is a development of the gland which begins to secrete the nectar; the evolution of the gland brings on the *atrophy* of the cell, but, fundamentally, there always remains an apparatus of *emission*.

Let us return to the Columbine: we have said that one way of transformation, and it is the most common one, would lead to a belief that the nectar-bearing sac may be in some instances the representative of a loculus of the anther. From

a slight examination we should in fact conclude so. As a proof of this, see the states delineated figures 3, 4, 5 and 6. We often see a stamen, with a filament dilated at its base, take two horns above (*c d*), whilst one loculus of the anther, inflated, no longer yields pollen; and the other, being atrophized to such a degree as no longer to appear except as a yellow gland (*b*), seems to have produced a rounded sac (*e*). This sac, the commencement of the cornet, should we not suppose it to be a modified anther-cell? and yet we have just seen that the tendency of the cells is to produce the lobes of the limb of the cornet, and not its tube. There is a mistake, indeed, as to the true signification of this enlargement, which is nothing but the middle of the connective itself. The connective extends itself outwards, and its hypertrophy brings with it the atrophy of the cells or of one cell of the anther; it signifies little whence substance comes to it, so that it only come. This is why the production of the spur does not always cause the whole anther to be metamorphosed all at once.

The better-formed cornets, and which even possess all the essential parts,—expanded limb, apex with two lobes and a slit, dilated faux, lengthened tube and terminal gland; these cornets, I say, sometimes still exhibit a trace of their old and primitive nature in the anther-cell, hardly visible, but distinguished by its yellow colour, whilst all the rest is white and blue, and, above all, distinguished by the grains of pollen that it still encloses in its bosom (fig. 4).

The conditions (figs. 5 and 6) are tendencies towards a regularized form of well-constituted nectaries. The condition (fig. 6) is that found in the common *Aquilegiæ*. Nothing here would lead to the supposition of an antherine nature, had not this strange metamorphosis been followed step by step.

It is evident, that all these cornets being hollow, and developed one above the other in several spirals (fig. 16), all likewise enter one into another (fig. 8), but it is inexact to say that then the glands no longer secrete. This is a mistake: the secretion continues, and, indeed, the tubes never completely close those into which they have entered.

Let us now examine in what manner the cornets are generated in a flower of *Aquilegia* taken at its first periods of development.

2. *Organogeny of the spur-shaped nectaries.*

To ascertain this organogeny, we have followed the method employed by Schleiden and Vogel. Taking a very young bud, which had hardly attained the length of a millimeter and

a half (fig. 10), we took off its calyx in water and with very fine needles. The central part then showed itself as a little sphere, whereon the stamina, having just quitted their form of green foliary gibbosities, now assumed that of two parallel protuberances (figs. 11 and 12). Upon these the connective is proportionally more developed than at a later period (fig. 12); the filament is dilated and very small; the anther is proportionally much larger, but it is still discoid, so that it is easier to discover in it the form of the blade of a leaf.

We were very curious to ascertain what the petals then were. The specimen which we dissected was one which would have had two rows of cornets. Now one of these rows (the exterior one) was formed by small circular laminæ, barely provided with a support, but these laminæ exhibited the same constitution as the anthers of the stamens described above (fig. 14): in fact, two gibbosities, representing the anther-cells (*a*, *c*); a very broad connective (*b*); and around all this a disc (*d*), of which, moreover, the trace also exists on the anther of a stamen proceeding in its development as such.

Here it is impossible to mistake the primitive staminal nature of the organ which at a later period is to become a hood-shaped petal, that is to say, a cornet-shaped nectary. It is evident that, after the first condition of the flower,—that in which all the parts were still cellular tubercles, similar to the primitive condition of a leaf,—the nectarial petal, before becoming such, was similar to a stamen. This is what caused us to say above, that the *spur-shaped nectaries of the Columbine did not produce stamens by ascending metamorphosis, but that they were, on the contrary, stamens modified by a descending metamorphosis.* In short, before being petals, they are rather stamens, or at least anthers, than anything else.

The row of small scales, which also become hood-shaped petals, but placed higher, exhibits at this age of the flower a more complete disappearance of the anther-like form. The anther betrays itself there only by the dilatation of the blade and its attenuated border (fig. 13 *b*), but there is but one common gibbosity in the place of the two parts which represented the loculi.

We took a bud three millimeters long (fig. 15), and stripped it of its calycinal envelopes. The stamens in this were better constituted, the filaments lengthened, the connective proportionally more contracted, and the loculi very distinct (fig. 17). The petaloid blades, on the contrary, were very broad, hardly pedicelled; but in the middle there is still the trace of the connective (*b*, fig. 19), and on the sides two protuberances, not so large, but prominent enough to discover in them the anther-

cells (fig. 19, *a*); traces or waves which incline us to suppose that there is a lateral extension of these cells to produce the petaloid lamina (fig. 19, *c*). It is evident that this is the anther flattening and dilating itself in order to become the petaloid lamina; and hardly does a bud attain the length of five millimeters before the laminæ are hollowed into tubes; and the spur-shaped nectaries, already making a projection outwards between the sepals of the calyx, are all formed (figs. 20 and 21).

This examination proves that, *in the genesis of the spur-shaped nectaries, Nature first forms a leaf, then a stamen, and that she converts the anther of this into a petal, at first flat and then hood-shaped.*

The nectary is then always a derivation from the stamen —*a descending metamorphosis of the stamen.*

This is precisely one of the facts which we have stated above. If it be to the detriment of the anthers that these singular spurs are produced in the Columbine, it was also a matter of interest for us to inquire if the laminæ noticed by DeCandolle between the carpels and the stamens are in reality abortive stamens. It is known that this author was in doubt concerning the nature of these organs. "One might say," he writes, in his 'Organography *,' "that they are either abortive stamens or interior petals." The latter opinion would be contrary to all the laws of Morphology previously established, for the corolline apparatus is exterior to the androœceum. However, to ascertain the true nature of these lamellæ, we have had recourse to an organogenic examination.

In a bud three millimeters long, we found these lamellæ composed (fig. 18) of a distinct base and summit. The summit is formed of two lateral swellings (*a b*, fig. 18), between which is a projecting lamella (*c*, fig. 18). The base is lamelloid and winged, with a nervure in the middle (*d*, fig. 18). There is here evidently a staminal structure: the swellings are the loculi of the anther, the projecting lamella the connective, and the lamelloid base the filament.

Now, in a well-developed flower, nothing remains of this summit, which becomes a true continuation of the lamella of the base. Thus the filament suffers hypertrophy, especially in breadth, and the anther, on the contrary, suffers atrophy. The base carries away the summit; the one pole as it dilates diminishes the other.

The *lamellæ* of the Columbine *are* then really *stamens modified by the annihilation of the pollen-bearing apparatus, and by the super-development of the filament.*

* Vol. i. p. 484.

It now became interesting, after these researches, to study what takes place in the tissues when the anther becomes a nectary. Our observations upon this we comprise in the following third chapter.

3. *Histology of the nectary.*

The anther is, as appears from the observations of Purkinje, Mirbel, &c., an apparatus characterized by a peculiar form of tissue. The endotheca, formed by fibro-cellular cells (inenchyme), hence affords a valuable means of distinguishing the part which the tissulary elements perform in metamorphoses. We were, for our part, greatly desirous of ascertaining this, after observation had convinced us that one stamen will change its nature and become a petal, and notwithstanding, will show in its interior tissue its first destination; whilst another stamen will modify its tissues along with its exterior form. We shall instance here, for the first of these cases, what we have seen in the *Reseda odorata, mediterranea, lutea, luteola,* &c. Our readers no doubt remember the interesting discussion on the nature of this flower between Dr. Lindley on one side, Mr. Robert Brown and Mr. Henslow on the other. Now in these flowers it is evident that the white filaments, which we have discovered to be the only organs of odour in this fragrant flower, are but modified stamens*. Indeed, we find in their interior, and especially at the upper end, an inenchymatous tissue, formed of fibre-bearing cells similar to those of the endotheca of an anther of the same plant,—indeed, identical with them. Now we do not think that a petal, properly so called, contains a similar tissue, excepting in some genera of *Orchideæ,* as the *Catasetum.* The staminal nature becomes quite evident by means of this entirely endothecal anatomy. In other plants, as for example in the *Pæonia officinalis,* where the stamen becomes a petal, nothing similar takes place. The tissue of the modified part is decidedly either altogether staminal (inenchymatous), or altogether corolline (cellular).

Purkinje had already made known the form of the inenchymatous cells of the endotheca of the *Aquilegia Gleberi*†. The fibres are radiated, oblique, and unite at the centre in a plate. The endothecal cells of the *Aquilegia vulgaris* (Plate XI. fig. 22)

* There is often a monstrosity in the *Reseda* which causes atrophy in the white filaments or the fringes of the petals. Then the flower is without any scent. No sooner are these fringes developed than the perfume begins to be perceptible. White colour in plants is often the indication of an agreeable scent. Here it is the stamens that grow white, in order to send forth a perfume.

† De Cellulis Antherarum fibrosis, p. 55. tab. xv. fig. 15.

are the same. They are stars, with diverging rays, to the number of eight or ten, which, seen from above, resemble the actinenchyme of Hayne. The junction of the radiating fibres takes place on a large plate (fig. 22, *b*).

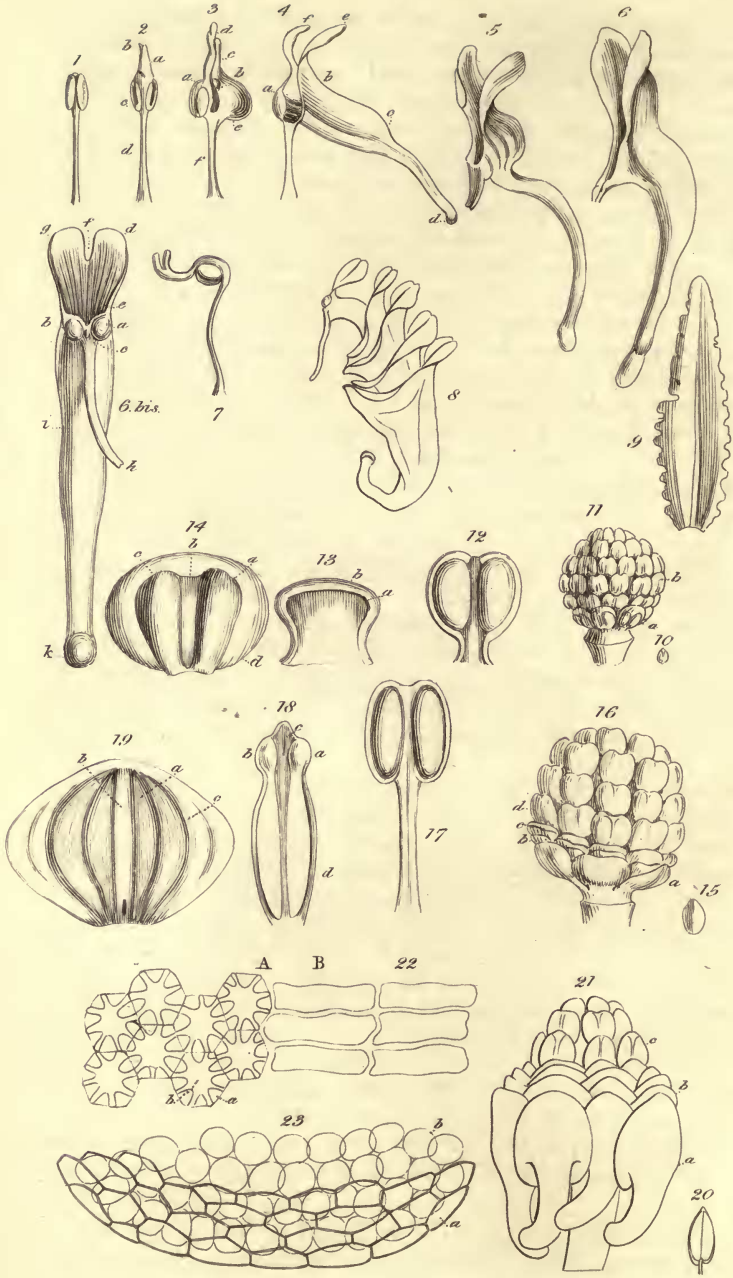
What becomes of this inenchymatous tissue in the metamorphosis of the anther into a spur? Does it continue with its form, as in the *Reseda*, or does it disappear, as in the *Pæonia*? With respect to this, observation shows, that the fibriferous cells lose their fibres at the same time that they change their form: from having been sphærenchyme this tissue becomes pinenchyme (fig. 22, A and B); and whilst the cell, from being spherical as it had been, becomes tubuliform, the fibre is resolved and disappears; its colour changes from yellow to blue, and instead of a star, only a blue liquid is seen there, without granules. I did not observe that the cytoblast, although my attention was especially fixed upon it, acted the least part in this histological metamorphosis.

When the spur is formed, the nectar-bearing gland appears like a mass of rounded cells (fig. 23 *b*), smaller and rounder than those of the derm (fig. 23 *a*).

The vascular system of the connective, on the contrary, performs an important part in this succession of changes of form, structure and function. Restricted at first, constituted by few fibres, in which we see fine tracheæ, hard to be unrolled, and pleurenchyme, this system soon divaricates its anastomoses, and fibres may be perceived in various directions, which, united, form an apparatus much larger than the primitive state.

It is evident from these researches, that the metamorphosis of the anther into a spur, that the change of the pollen-bearing apparatus into the nectar-bearing apparatus, attack the deepest tissues, and that if a morphological metamorphosis takes place, an histological metamorphosis takes place also. If the functions change, there is, as we see, a phænomenal translation of this change by that which exists most intimately in the organization—the tissular constitution. Cases of metamorphosis, indeed, only become interesting to the physiologist, when he comes to know what at the same time is passing in the tissues. We may therefore say here, that *if, in the Columbine, the connective forms the nectar-bearing spur, this change leads to the metamorphosis of the inenchyme of the anther-cells into parenchyme*, and that *the metamorphosis attacks in as great a degree the entire organism as the tissues which compose it.*

We have now to add a few words relative to the varieties of *Aquilegiæ* called *stellated*. DeCandolle attributes the peta-



Aquilegia vulgaris.

Ch. Morren del.

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